

Decline of Mammal Species Diversity Along the Yungas Forest of Argentina

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ABSTRACT

The southernmost extension of tropical Andean–Amazonian forests protrudes into the arid to semiarid habitats in northwestern Argentina. We analyzed the decline of species richness of forest mammals along these Yungas forests. In particular, we tested whether species decline is due to a general latitudinal effect and whether the drop of species from the assemblages was independent from species' traits and environmental variables. For these tests, we estimated the geographic range edges of 39 species of forest mammal and estimated the species richness with bands of 30'. First, we compared the slope of the decline of species richness from north to south (5.8 species/degree) with the decline expected from the latitudinal species gradient (1–3 species/degree). The decline in species richness of forest mammals along the Yungas was significantly steeper than expected. Second, with a null model assuming a random drop of mammal species we derived confidence limits for the expected species richness and number of range edges within the bands. None of the forest mammals reached the tip of the forest, in marked contrast to nonforest mammals. More range edges than expected from the null model fell within the bands 23°30'–24°00' S and a band near the tip of the Yungas indicating a nonrandom drop of species. The correlation between vulnerability traits and range edges suggests that processes associated with the availability of resources influence the drop of species. We propose that a suite of macroecological attributes interacting with a decrease in habitat quality determines the pattern of species richness in the Yungas forest.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: fragmentation; geographic range edges; macroniches; Neotropical forest mammals; North West Argentina; tropical–temperate ecotone; vulnerability.

MORE THAN 40 YEARS AGO, Simpson (1964) noted that species richness declines from the base to the tip of peninsulas. A number of subsequent studies reported similar patterns across many taxa, but also some exceptions (*see* Wiggins 1999 and references therein). Simpson argued that the decline in species richness along peninsulas is due to the effect of the peninsula's geometry on the immigration and extinction rates. Soon after MacArthur and Wilson (1967) published their influential ideas on island biogeography, ecologists and biogeographers realized that 'islands' may not only be pieces of land surrounded by water like oceanic islands, but also patches of a certain habitat embedded within a matrix of a different habitat (Wilson & Willis 1975, Brown 1978, Laurance & Bierregaard 1997, Ricketts 2001, Shepherd & Brantley 2005 and references therein). Typical for such a situation are patches of forest within grasslands, or remnants of forests within an otherwise agricultural area.

The southernmost extension of Andean tropical forests is discontinuous and interdigitate from southern Bolivia into a matrix of temperate arid–semiarid landscapes in northwestern Argentina. The

local name of the forests is 'Yungas' (Ojeda & Mares 1989, Ojeda 2000; Fig. 1). Several studies on plants, amphibians, lizards, birds, and mammals reported a north–south decline of species richness along these Yungas forest (Rabinovich & Rapoport 1975, Ojeda & Mares 1989, Morales 1996, Capllonch 1998, Lavilla *et al.* 2000, Ojeda 2000, Brown *et al.* 2001). However, as the Yungas forests are oriented from north to south, some decline of species richness is expected from the well-known latitudinal gradient of species richness (Hillebrand 2004). For forest species, the Yungas form a sort of a peninsula and an understanding of the species decline may contribute not only to a better understanding of tropical forest biogeography but also to the conservation of biodiversity in the Yungas and rain forest in general. There is no doubt that the tropics is facing an accelerated rate of deforestation, and that remnants of forest are becoming the dominant feature in many tropical biodiversity hotspots (Laurance & Bierregaard 1997, Myers *et al.* 2000). However, most of the studies on the decline of species richness along the Yungas forest were qualitative or semi-quantitative. Few studies distinguished between forest and nonforest taxa.

The purpose of the present paper is to quantify the decrease in species richness of the forest mammals along the Yungas of

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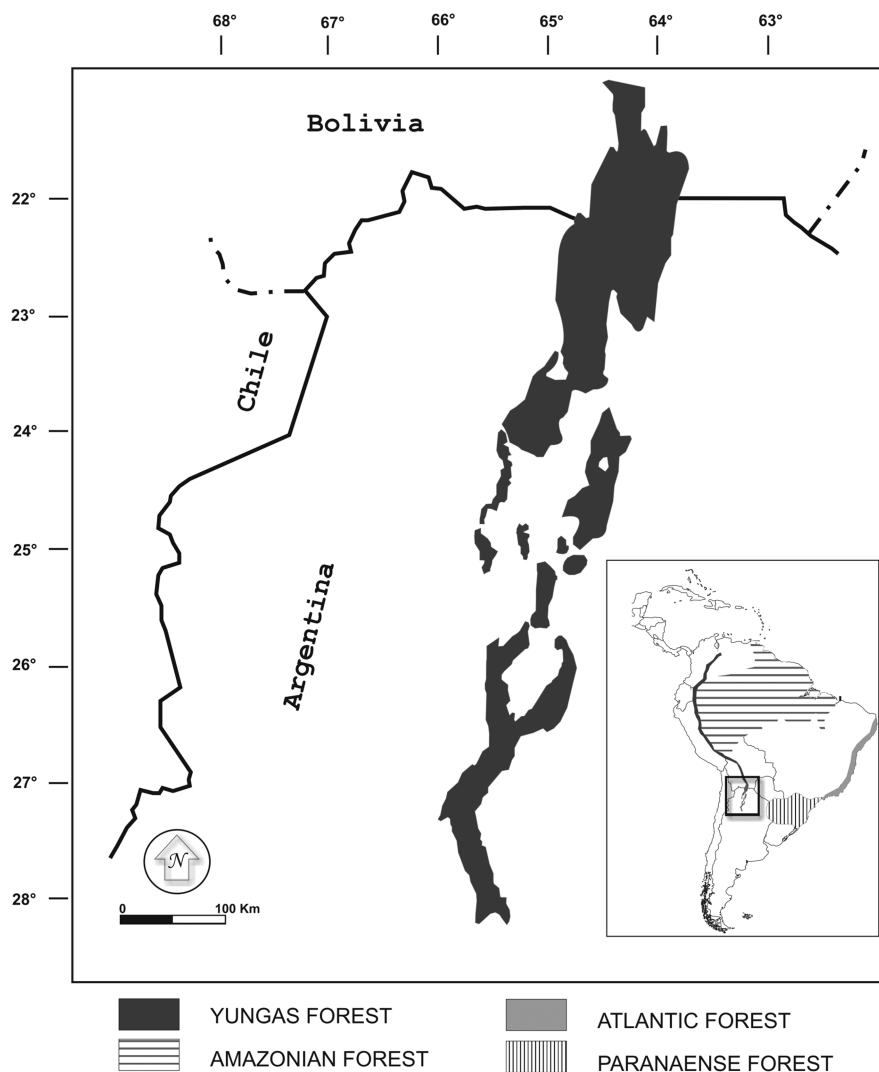


FIGURE 1. Map of the Yungas forest between 22° and 28° S in northwestern Argentina and other South American tropical and subtropical forests (After Brown *et al.* 2001).

northwestern Argentina. With these data, we test the following hypotheses: (1) due to the north–south placement of the Yungas, the species richness of forest mammals follow the same rate of species' loss as the nonforest species and the decline of species is according to the general latitudinal gradient in species richness; and (2) the drop of forest species is random in respect to characteristics of the Yungas as well as traits of species. For a test of this hypothesis, we developed a simple null model and analyzed the correlation of ecological traits with the position of range edges along the Yungas forest.

METHODS

The tropical mountain cloud forests extend along the eastern versant of the Andes, from northern Venezuela (8° N) to north-

western Argentina (29° S) and belong to the Amazonian domain (Cabrera & Willink 1973; see also Fig. 1). At their southernmost limit, these forests comprise the phylogeographic province of the Argentine Yungas (Cabrera 1976). These forests, locally known as the 'selva tucumano-boliviana' and running between 18° S up to 29° S, are recognized as a distinct biogeographical and ecological unit. These forests are structured into several strata composed of tall trees (20–30 m in height), shrubs, lianas, epiphytes, and grasses (Grau & Brown 2000, Brown *et al.* 2001, Kessler & Beck 2001). Rainfall is seasonal (dry winter and wet summer seasons) and varies from 700 to 2000 mm, with an average annual temperature of 21°C.

We concentrated our study on the southernmost extension of the forests between 22° S and 29° S. Distribution data of the yungas mammals were based primarily on our own records, either published

or new, and pertinent references (Ojeda & Mares 1989; Redford & Eisenberg 1992; Barquez *et al.* 1999; Ojeda *et al.* 2002, 2003; Barquez *et al.* 2006). Our data base was composed of georeferenced records with voucher specimens in major scientific collections (see Ojeda & Mares 1989, Barquez *et al.* 1999, Diaz 1999, Ojeda *et al.* 2003). Most distributional ranges of species included in our analysis extend from Mesoamerica and tropical northern South America, to northern Argentina. We focus our analyses on 39 mammal species occurring only in forests (Ojeda *et al.* 2002, Barquez *et al.* 2006). Additionally, we consider 74 nonforest mammals in some of the analyses for comparative reasons (the complete list of forest and nonforest Yungas mammals is available upon request from R. Ojeda). For our analysis, we considered the southernmost record of each forest species as its southern range edge. From these range edge data, we calculated the species richness of forest mammals within latitudinal bands of 30' assuming that the species occurs in all bands north of the range edge. Total forest area and number of major fragments of forests within each latitudinal band were estimated from Figure 1. A regression of species richness within bands versus latitude of bands provides an estimation of species loss. Species richness of adjacent bands is not independent and therefore we estimated confidence limits for the slope using 4000 bootstrap samples.

If one assumes a random drop of forest species from the mammal communities along the forest peninsula, the expected number of range edges within each band is identical. To calculate the confidence limits (90%), we performed simulations where we placed range edges of species at random between the northern portion of the Argentine Yungas (at 22°) and the tip (at 29°) drawn from a uniform distribution. Four thousand assemblages, of 39 species each, were generated by selecting for each species at random a range edge between 22° and 29°. From these random draws, we estimated confidence intervals for the decline of species richness (see also Means & Simberloff 1987). These intervals around the expected values allow for a simple statistical evaluation as to whether observed values deviate significantly from the expectation.

We used body size (\log_{10} transformed) as well as biological attributes (adapted from the SUMIN index; see Reca *et al.* 1994, 1996) to characterize the degree of vulnerability of forest species. These traits were ranked as follows: geographic range at continental scale, from 0 (distributed continentally) to 3 (restricted distribution); geographic range at national scale, from 0 (found throughout Argentina) to 5 (restricted distribution); habitat use: from 0 (occurs in more than one habitat type) to 2 (restricted to one habitat type); reproductive potential, 0 (high) to 2 (low); trophic level, 0 (omnivores, generalist herbivores) to 2 (specialists, carnivores); and abundance 0 (abundant or common) to 2 (rare). We generated a vulnerability index by summing up the ranks of each species across components. Each mammal species was assigned to a macroniche category (Ojeda & Mares 1989). For all statistical analyses as well as the simulations we used the platform R (R Development Core Team 2004) using the appropriate functions (see also Venables & Ripley 2002).

RESULTS

The Yungas forest shows a decrease in area from north to south, and is particularly discontinuous (fragmented) between 25°00' to 25°30' latitude (Figs. 1 and 2). Our analyses include 39 mammal species restricted exclusively to forests within our Yungas study area (Table S1). In general, we found a decrease in mammal species

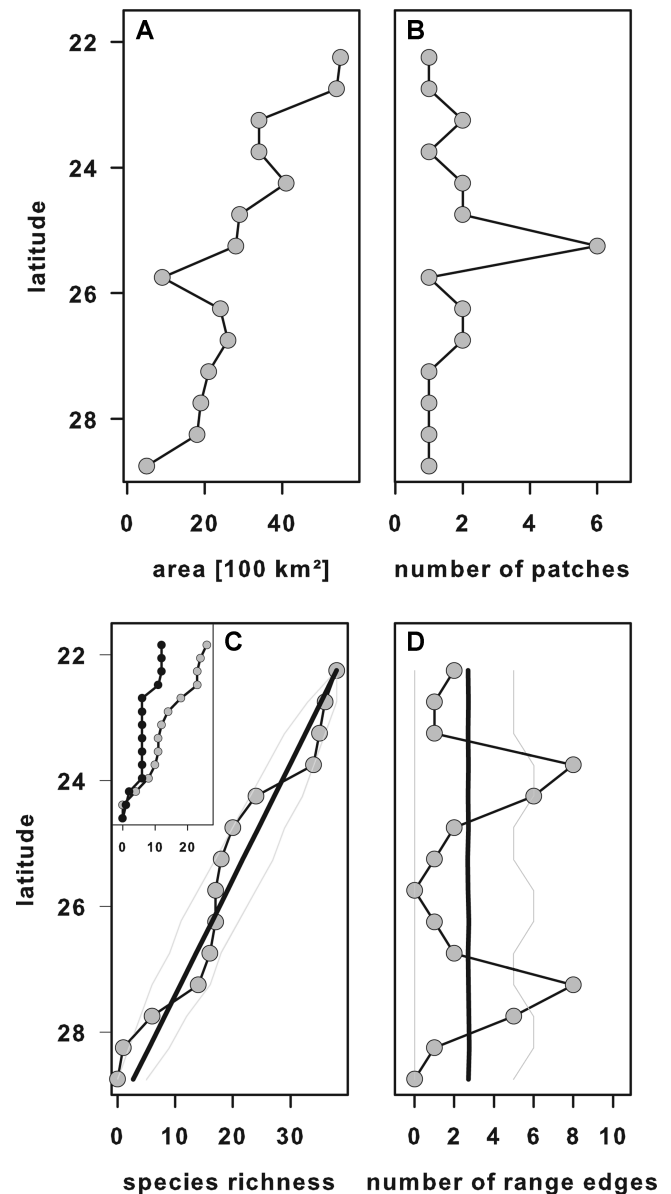


FIGURE 2. Plots of forest area, number of forest fragments, species richness, and number of range edges within latitudinal bands of 30'. For species richness and number of range edges we give the expected values and associated 90% confidence limits derived from simulations with a random placement of range edges along the peninsula. The inset shows the decrease of species richness for bats (black symbols) and nonvolant species (gray symbols).

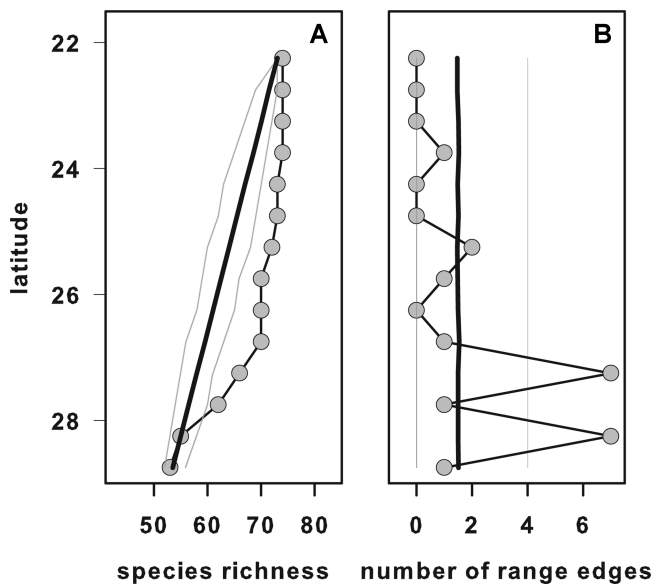


FIGURE 3. Plots of species richness for nonforest mammals as well as number of range edges within latitudinal bands of 30'. For species richness as well as number of range edges we also give the expected values and associated 90% confidence limits derived from simulations with a random placement of range edges along the peninsula.

richness along the forest. None of the forest mammals reached the tip of the forests at 29° latitude, whereas only 21 nonforest mammals did not reach the southernmost parts of the Yungas in Argentina (Figs. 2 and 3). Ranges of tropical-Amazonian species of phyllostomid bats, primate (*Cebus apella*), sciurid (*Sciurus ignitus*), and several hystricognath rodents such as dasyproctids *Dasyprocta* and porcupines (*Coendou*) extended not beyond 25° latitude. Using simple regression, the slopes of the decrease of species richness along the Yungas were -5.8 (95% CI: -6.3 to -5.4 ; $r = -0.97$) for forest mammals and -3.0 (-3.4 to -1.6 ; $r = -0.87$) for nonforest mammals. These slopes are statistically different (ANCOVA $F_{1,24} = 22.1$; $P < 0.001$). However, such test using species richness within bands as independent values is not strictly valid (df overestimated). However, the confidence limits estimated with bootstrap samples did not overlap also indicating a significant different decline of forest and nonforest mammals along the Yungas.

Species richness of forest mammals was always within the 90 percent confidence band estimated from a random placement of range borders. However, the number of range edges within each band showed a clear nonrandom pattern, as more range edges were located within the latitudinal bands of 23° and 27° than expected by chance (*i.e.*, lie outside of the confidence limits; see Fig. 2). For nonforest species, species richness decreased decreases at the tip of the forests. More nonforest mammals than expected by chance had their range edge near the tip of the Yungas forest (Fig. 3). Range edges of forest mammals were not related to latitude, area, and degree of fragmentation, whereas for nonforest mammals there was a significant association with latitude (Table 1).

TABLE 1. Generalized linear models for the number of range edges within latitudinal bands (breadth 30'; 14 bands; Figs. 2 and 3; Poisson error) vs. latitude, forest area within bands, and number of forest fragments. The first band is between 22° 00' and 22° 30', the last between 28° 30' and 29° 00'. The variance inflation factor (residual deviance divided by residual degrees of freedom; df) is < 4 and therefore we have not corrected for overdispersion. We tested the effects sequentially.

	df	Forest mammals		Nonforest mammals	
		Deviance	P	Deviance	P
Latitude	1	0.08	0.78	16.8	< 0.001
Area	1	2.1	0.15	1.6	0.20
Number of fragments	1	1.7	0.20	0.4	0.53
Residual deviance	10	32.7		21.4	

The forest mammals are distributed among 17 macroniches (see Table S1). This functional diversity also decreased along the forest. Forty-seven percent of the macroniche categories did not reach the tip of the Yungas forest (in particular volant nectarivores, and arboreal, scansorial, or terrestrial frugivore-granivores). In general, forest species with high vulnerability indices, and small body sizes dropped early from the mammalian assemblages along the Yungas forests (Fig. 4; Table 2).

DISCUSSION

Several studies reported a decline of species richness (*i.e.*, plants, amphibian, lizards, and birds) along the southernmost extension of the Yungas forest, although not all studies distinguished between forest and nonforest taxa (Rabinovich & Rapoport 1975, Morales 1996, Capllonch 1998, Lavilla *et al.* 2000, Brown *et al.* 2001). We found a clear difference in the decline of forest and nonforest mammals. Moreover, our results show a nonrandom pattern in the decline of species richness, which we were able to show is associated with certain traits of species.

The Yungas forest is oriented in a north-south direction and one may expect a decrease of species richness simply because there is a latitudinal gradient in species richness from low to high latitudes. To test whether one may explain the observed decline of forest mammals by a latitudinal effect, we estimated the decrease of species richness for each degree of latitude (Table 15.1 in Brown & Lomolino 1998; Fig. 3 in Hillebrand 2004). The decrease of non-volant and volant mammals expected from these two sources ranges between one and two (Hillebrand 2004) and 2.3 species (Brown & Lomolino 1998) for each degree of latitude. For the Yungas forest species, we found a decrease of 5.8 species/degree, a much steeper decline than expected from a latitudinal gradient of diversity. Furthermore, the expected decline falls outside the confidence limits of the decline observed for the forest mammals (decline between 5.4 and 6.3). Interestingly, the decrease of nonforest mammals was

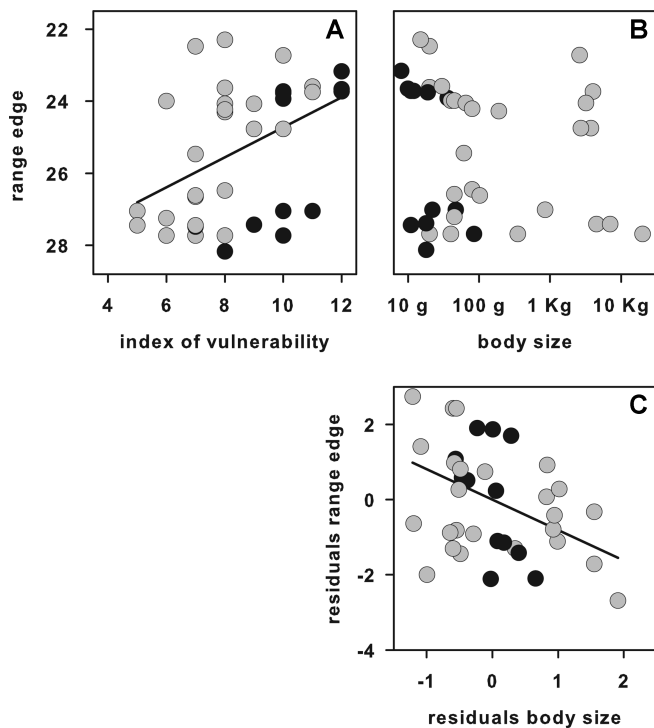


FIGURE 4. Plot of vulnerability index and body size versus position of range edges. Filled symbols for bats and gray symbols for nonvolant species. The regression line gives the regression line across all points. For body size we also plot the residuals of body size and range edge after accounting for vulnerability and the factor bats versus nonvolant species. This relationship is equivalent to the test presented in Table 2.

about three species per latitudinal degree, much closer to the general latitudinal trend and the general latitudinal trend is within the confidence limits (decline between 1.6 and 3.0). Clearly, the decrease of forest mammals is not simply a latitudinal effect.

Previous research (Ojeda & Mares 1989, Ojeda 2000) suggested a peninsular effect (Simpson 1964), but without any quantification of the species' range edges and variables involved in the pattern. Despite the differences between real (*e.g.*, California, Florida, among others) and continental 'peninsulas' (*i.e.*, Yungas forest) we consider a useful analogy in order to dissect some of the ecological processes that might be operating in our study area. A decrease of species richness along real peninsulas might be based on several processes such as historical constraints, extinction-recolonization dynamics, and habitat diversity (*see* Wiggins 1999 and references therein). The age of the subtropical Yungas forest of Northwestern Argentina and Bolivia dates to the end of Miocene-Pliocene (Hinojosa & Villagran 1997). From documented range expansions of invasive mammals, we know that species may spread *ca* 10–20 km/year (Hengeveld 1989). By extension, considering that the Yungas is approximately 700-km long (22° to 29°), it would take about 70 yr for such a species to reach the southern tip. Moreover, species with very different vagilities (*e.g.*, volant vs. nonvolant mammals) show a similar decrease of species richness. In fact, 50 percent of the bats have distributional limits of 23–24°. Hence, historical

TABLE 2. General linear model with the location of range edges as dependent variable, and vulnerability index and body size (\log_{10} -transformed) as independent variables. Species were grouped into bats and nonvolant species (type I sum of squares).

Source	df	Mean SS	F	P
Bat/nonvolant	1	0.58	0.27	0.61
Vulnerability	1	45.8	21.2	< 0.0001
Body size	1	15.9	7.35	0.01
Bat/nonvolant \times vulnerability	1	0.24	0.11	0.74
Bat/nonvolant \times body size	1	3.19	1.47	0.23
Body size \times vulnerability	1	0.48	0.22	0.64
Bat/nonvolant \times vulnerability \times body size	1	< 0.01	< 0.01	0.96
Residuals	30	2.16		

constraints fail to account for the decline of forest mammals along the Yungas forest.

The immigration-extinction hypothesis implies that the geometry of the peninsulas with its effects on the extinction and especially immigration rate is the cause of the decrease in species richness as a function of distance (Simpson 1964, Means & Simberloff 1987). Simulations performed by Taylor and Regal (1978) showed that extinction and immigration process would generate a pattern of species richness with a steep decline near the base, followed by a plateau and a decline near the tip, whereas Gilpin and Diamond (1981) showed a gradual decline of species richness. Our results do not show the pattern expected from Taylor and Regal's simulations, although the species richness of bats along the peninsula came close to the predicted pattern. The immigration-extinction hypothesis also implies that species with different dispersal abilities should show different patterns in the decline along the forest (*i.e.*, volant mammals should extend farther than nonvolant species). Our results point even to an opposite direction (Fig. 2 inset).

The Yungas is a discontinuous (fragmented) forest between 25° and 25°30' S, and this may have acted and actually might act as a filter for the more vulnerable tropical species (*see* Fig. 2; Terborgh & Winter 1980). However, the band with the peak of range edges did not coincide with the location of the forest fragments (Fig. 2) and we found no positive correlation between the number of forest fragments and the number of range edges within the analyzed bands. However, field records may not portray actual range edges. Palaeontologists dubbed this effect 'Signor-Lipps effect' or 'backsmearing' in palaeontology (Signor & Lipps 1982): species records are unlikely to represent the actual range limits and therefore all estimates of species ranges are truncated to some extent. Furthermore the correlation between vulnerability traits, body size, and the position of range edges suggests that certain habitat factors (*i.e.*, a general decrease in habitat quality) are associated with the drop of certain species from the assemblages. A general decrease in habitat quality for mammals along the Yungas is also reflected in the decline of species richness in pteridophytes, from 37–40 (at 22° S) to 16–20 (at 28° S), as well as in the decrease of tree species, from 167 to 79, and an increase in seasonality (*i.e.*, number of months

with frost; Brown *et al.* 2001). The southernmost range edges for several tropical genera (*e.g.*, *Cebus*, *Dasyprocta*, *Sciurus* or *Coendou*, *Anoura*, *Glossophaga*, *Tonatia* and *Pygoderma*; see Table S1) suggest that certain keystone food resources (*e.g.*, nectar, fruits of *Ficus* trees) or ecophysiological limitations due to an increased seasonality and unpredictability of resources at the tip of the Yungas forest (Ojeda & Mares 1989, Laurance 1991) constrain the occurrence of species (*e.g.*, nectarivores; see Terborgh & Winter 1980, Arita & Santos del Prado 1999) leading to a truncation of ecological guilds (Wilson & Willis 1975; Laurance 1991, 1997; Corlett 2000). The negative relationship might also be the result of particular vulnerability of small mammals dependent on resources such as nectar and fruits (Terborgh & Winter 1980, Arita & Santos del Prado 1999). These resources might be rare after unusual cold or dry seasons. We found that, with increasing body size, species were able to protrude more to the south. In part, this pattern is based on a few large-bodied species (> 6 kg) with special attributes (*e.g.*, *Lutra longicaudis* dispersing along rivers, or the brocket deer, *Mazama americana*, restricted to upper montane forest habitats; Ojeda & Mares 1989, Mares *et al.* 1991).

Although the factors involved in delimiting the species borders of distribution (*e.g.*, range edges) are extremely complex and diverse (*see* Gaston 2003, and references therein), our results suggest that the decline in species richness along the Yungas results from the combination of a decrease in habitat quality (*e.g.*, fragmentation or discontinuous blocks of forest; decreased vegetational richness and complexity; increased seasonality) in interaction with biological and macroecological attributes of tropical mammals at their geographic range edges. A factor that deserves close attention during future work is the relationship between range edge and population abundance. Density declines toward the periphery of a species' geographic range (Brown 1984; Hengeveld & Haack 1982). Therefore, populations at the periphery of their ranges should be more prone to local extinctions compared to the range center (Ceballos & Ehrlich 2002).

The conversion of the tropical montane forests due to logging, fragmentation, agriculture expansion, land-use conversion for new crops (*e.g.*, GM soybean), oil and gas exploration and extraction, proceeds at an accelerated pace (Hamilton *et al.* 1995). This will enhance the natural isolation of the Yungas forest blocks, increasing the risk of local extinctions, and thereby the truncation of certain macroniches (Ojeda 2000, Corlett 2000). At a local level, particular attention should be given to those species restricted to forest habitats and characterized by low rate of occupancy (*i.e.*, rarity; Ojeda *et al.* 2003, Tabeni *et al.* 2004). Among these, the frugivore–nectarivores, arboreal and carnivores should be closely monitored. Needless to say, a new blueprint on land use and planning of biodiversity conservation based on the tools provided by biogeographical principles and theories (Whittaker *et al.* 2005) is urgently needed if the Yungas forest is going to remain functioning as the southernmost tropical ecosystem of the Andean–Amazonian biota.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

TABLE S1. *Forest mammals of the Yungas in northern Argentina. The table presents the co-ordinates of their southernmost occurrence, body mass, vulnerability index, and macroniche.*

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